Contrasting effects of short-term litter removal on soil respiration in native Phragmites australis and exotic Spartina alterniflora marshes

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Abstract

Salt marshes produce substantial amounts of plant litter, playing a vital role in the long-term accumulation of soil organic carbon. However, the influences of plant litter on soil respiration in salt marshes remain largely unclear, especially when global salt marshes are threatened by plant invasion. We conducted a field experiment to examine how litter removal impacts soil respiration through soil physicochemical properties (temperature, moisture, pH, salinity, inorganic nitrogen, organic carbon) and plant growth (height, density, aboveground biomass) in native *Phragmites australis* and exotic *Spartina alterniflora* salt marshes. The results indicated that litter removal had contrasting effects on soil respiration in the before and after *S. alterniflora* invasion. In *P. australis* marshes, litter removal decreased soil respiration by 38.3% due to increased soil salinity, while in *S. alterniflora*, it enhanced soil respiration by 25.9% through increased AGB. Although the litter removal can affect level of soil inorganic nitrogen, pH and organic carbon, these are not the main factors that alter soil respiration. The study highlights that plant litter plays a crucial role in driving Rs in salt marshes, and the processes change with plant invasion. In the future, to accurately predict the carbon cycle process of salt marshes, it is necessary to comprehensively consider the complex relationships among vegetation types, litter, and soil properties.

Introduction

Salt marshes sequester significant amounts of carbon within a small terrestrial area, driven by high plant productivity and anaerobic limit organic carbon decomposition rate (McLeod et al. 2011, Duarte et al. 2013). Soil respiration (Rs) is a major pathway of carbon (C) exchange between ecosystems and the atmosphere, playing an important role in the ecosystem C balance (Bond-Lamberty et al. 2018). In salt marshes, Rs is highly sensitive to environmental changes and can be influenced by various biotic and abiotic factors, including soil temperature, flooding, nutrient availability, vegetation types, and plant litter inputs (Chambers et al. 2013, Bu et al. 2015, Vivanco et al. 2015, Wang et al. 2021a). Given their vital role in carbon sequestration, understanding the mechanisms underlying Rs responses to these factors is crucial for predicting the future of salt marsh C budgets.

Plant litter, comprising dead stems, leaves and roots, is a primary source of soil organic matter and a key regulator of biogeochemical C cycling. In many terrestrial ecosystems, increased litter input generally enhances Rs, for instance, through priming effects or direct C substrate provision (Shahzad et al. 2015, Wu et al. 2017, Wang et al. 2021b), while litter removal often reduces Rs by limiting substrate for decomposition (Li et al. 2022, Bethe et al. 2025). Beyond these direct C contributions, plant litter indirectly affects Rs by modulating soil abiotic properties and consequently influencing plant community dynamics and growth. For instance, litter input increases the availability of soil nutrients through increasing organic matter decomposition and mineralization. Moreover, plant litter can regulate the soil microclimate by creating a buffer interface between the soil surface and the atmosphere, influencing soil temperature and humidity (Sayer 2006, Fekete et al. 2015, Zhang et al. 2025). Subsequently, the changes in the soil environment brought about by the litter removal can affect the growth of plants (Leff et al. 2012, Rodtassana and Tanner 2018, Heim et al. 2021). Studies show that the removal of litter reduces productivity by increasing the bare surface area, solar radiation intensity, and soil water evaporation (Sharma et al. 2012, Hou et al. 2025). These alterations in plant growth can, in turn, modify rhizosphere carbon inputs, creating complex feedback loops (Zerihun and Montagu 2004). However, the mechanisms of plant litter on Rs in salt marsh ecosystems remain less understood and potentially distinct from other terrestrial systems.

The influence of plant litter on Rs can be strongly modulated by prevailing environmental conditions. For instance, moisture limitations in European deciduous forests negated the expected Rs increase from litter additions (Fekete et al. 2014). Another study in pine forestland shows that, the stimulation of nitrogen on soil greenhouse gas emissions exceeds the inhibition of litter removal to that (Fan et al. 2020). Therefore, the impact of litter on Rs cannot be determined solely by the direct and indirect effects of organic matter input, but also influenced by other environmental conditions. In salt marshes, the unique interplay of tidal inundation (leading to periodic anoxia) and high soil salinity likely alters the decomposition pathways and microbial communities, thereby shaping the contribution of litter to Rs in ways that differ from better-studied upland ecosystems (McLeod et al. 2011, Campbell et al. 2022). These distinctive characteristics highlight the necessity of investigating Rs responses to litter manipulation in salt marsh ecosystems.

Furthermore, coastal wetlands worldwide are increasingly impacted by biological invasions, often facilitated by human activities and climate change (Diagne et al. 2021). Certain invasive plant species, recognized for their exceptional environmental tolerance and adaptability, have proliferated extensively in these ecosystems (Liao et al. 2007, Wang et al. 2008, Wu et al. 2008, Lin et al. 2024). Invasive plants often exhibit higher primary productivity than native communities and produce greater amounts of plant litter (Ehrenfeld 2010). Furthermore, invasive species can alter the quality of plant litter (Huang et al. 2016). These invasion-induced changes in both the quantity and quality of litter could lead to divergent effects of litter on Rs between native and invaded salt marshes, yet this aspect has received limited attention.

Here, we conducted a field experiment in the Yangtze River estuary, where exotic *Spartina alterniflora* has extensively invaded native *Phragmites australis* marshes (Liao et al. 2008). This setting provides an ideal opportunity to investigate how plant invasion modulates the role of litter in soil carbon cycling. We aimed to determine the contrasting effects of short-term litter removal on Rs in these native and invade salt marshes, and to elucidate the underlying mechanisms by examining concurrent changes in soil physicochemical properties and plant growth. Specifically, we hypothesized that: (1) litter removal would significantly affect Rs in both native and exotic salt marshes, but the direction and magnitude of this effect would differ between the two marsh types; and (2) these contrasting responses would be driven by distinct alterations in key soil properties (e.g., salinity, nutrient availability) and plant growth performance (e.g., aboveground biomass) induced by litter removal in each marsh type.

Materials and methods

Study area

The study was conducted in a salt marsh on Chongming Island, located at the Yangtze River Estuary, Shanghai, China (31°41'35.03" N, 121°39'22.69" E; Fig. 1). This region has a typical subtropical monsoon climate, with a mean annual temperature of 15.3°C (monthly means ranging from 2.9 ~ 27.5°C) and a mean annual precipitation of 1022 mm (primarily occurring between April and September). Tides are regular and semidiurnal, with an average tidal range of 2 to 6 m (Huang et al. 2016). The study focused on areas dominated by the vascular plant species *P. australis* and *S. alterniflora*.

Experimental design

To evaluate the effects of litter removal on Rs in native and invade salt marshes, we conducted a litter manipulation field experiment from December 2018 to December 2019. In December 2018, two parallel transects, approximately 250 m apart, were established. Each transect was approximately 200 m in length and contained ten 4 m^2 (2 × 2 m) plots, resulting in a total of twenty plots. Plots within each transect were spaced at least 15 m apart to ensure spatial independence. The experiment employed a two-factor design: litter manipulation (litter removal vs. control) and plant community type (*P. australis* marsh vs. *S. alterniflora* marsh). This resulted in four treatment combinations: (1) *P. australis* control, (2) *P. australis* litter removal, (3) *S. alterniflora* control, and (4) *S. alterniflora* litter removal, with five spatial replicates for each treatment (Fig. 1). Litter removal and control plots for each plant community type were spatially paired. In the litter removal plots, all existing aboveground litter and plant detritus were carefully removed using sickles at the beginning of the experiment (December 2018). Subsequently, any newly fallen litter was gently raked and removed from these plots at monthly intervals throughout the study period. Control plots remained undisturbed with natural litter accumulation.

Plant density, height, and aboveground biomass

Plant characteristics were assessed at the peak of the growing season in mid-October 2019. In each plot, plant density was determined by counting the number of ramets in a central quadrat (0.5 × 0.5 m for *P. australis*, and 0.3 × 0.3 m for *S. alterniflora*). Plant height of ten randomly selected ramets per plot was measured using a stainless tape measure. Subsequently, aboveground plant material within the central quadrat was harvested by cutting at the soil surface. In the laboratory, harvested plant tissues were rinsed with tap water to remove adhered soil and debris. Samples were then placed in an oven, initially at 105℃ for 2 hours to rapidly halt metabolic activity, followed by drying at 80℃ to a constant weight. The total dry weight of all aboveground plant tissues per quadrat was recorded as aboveground biomass (AGB).

Soil physicochemical properties

Soil samples were collected in October 2019. In each plot, three soil cores (8 cm diameter) were randomly taken from the 0–15 cm depth layer, ensuring samples were at least 10 cm away from Rs collars and plot edges to minimize disturbance. Soil cores from same plot were combined to form one composite sample. Composite samples were transported to the laboratory in a cooler and then stored at -20℃ until analysis. Prior to analysis, samples were thawed and sieved through a 2 mm mesh to remove stones and coarse roots; a total of twenty composite soil samples were processed. Soil moisture content was determined gravimetrically by oven-drying a subsample of fresh soil at 80℃ until constant weight. Soil organic carbon (SOC) concentrations were measured on oven-dried ground soil samples using an elemental analyzer (FlashSmart NC, Thermo Fisher Scientific, USA). Soil ammonium (NH + 4) and nitrate (NO- 3) were extracted from fresh soil subsamples using a 0.5 mol L^{-1} K_2SO_4 solution. Their concentrations were determined colorimetrically using the salicylic acid and molybdate blue methods, respectively, with a microplate reader (Synergy H2, Bio Tek, USA). Soil pH and salinity were measured in a 1:5 (dry soil weight: deionized water volume) suspension using a modular multi-channel pH/conductivity meter (SevenExcellence S479-uMix, Mettler Toledo, Switzerland).

Soil respiration

We measured Rs from April to December 2019 using a closed-chamber method with a portable automated Rs system (LI-8100, Li-Cor Inc., USA). In each plot, one white PVC collar (200 mm inner diameter, 300 mm height) was permanently installed at the center, inserted approximately 50 mm into the soil at the beginning of the experiment. Pipes remained in place throughout the study to minimize soil disturbance. At least one day prior to each Rs measurement, any live plant seedlings or green shoots within the collars were carefully removed by hand, and visible crab burrows were gently filled with surrounding soil to minimize their influence on CO_2 efflux. Rs measurements were typically conducted between 09:00 and 11:00 AM on days following neap tides, weather permitting, to ensure comparable tidal conditions. For each measurement, the LI-8100 chamber was sealed onto a PVC collar for 90 seconds to record the rate of CO_2 concentration change. Simultaneously, soil temperature and moisture at a 10 cm depth adjacent to each pipe were recorded using sensors connected to the LI-8100 system.

Litter decomposition

In April 2019, 20g of dried litter were placed in nylon mesh bags (mesh size 1 mm) and placed on the soil surface. On the 30th, 130th, and 210th day, the bags were collected, the soil on the litter was gently washed off. After 80℃ dried, the litter mass remaining and decomposition constant (*k*) were calculated.

Litter mass remaining = $((Mass_{initial}-Mass_{final})/Mass_{final})/t$

Decomposition constant (*k*) = $\ln(Mass_{initial}/Mass_{final})/t$

Statistical analyses

One-way ANOVA was used to test the differences in plant characteristics and soil physicochemical properties between treatment plots. Two-way ANOVA was utilized to evaluate the effects of salt marsh type, litter removal, and their interaction on plant growth and Rs. A repeated-measures ANOVA, with litter treatment as the between subject factor and measurement date as the within subject factors was conducted to examine effects of litter removal on seasonal dynamics of Rs and Litter decomposition. Least Significant Difference (LSD) method was applied to assess the effects of litter removal on soil properties. General linear modeling was used to fit the relationships between AGB, soil physicochemical properties, and Rs. All data analyses were conducted in the R version 4.0.5 software.

Results

Effects of plant community type and litter removal on soil physicochemical properties

Initially, we observed significant differences in baseline soil properties between the two marsh types in control plots (Table 1). *P. australis* marshes exhibited significantly higher soil moisture and pH compared to *S. alterniflora* marshes (all $p < 0.05$). Conversely, *S. alterniflora* marshes had significantly higher soil temperature, soil salinity, soil organic carbon (SOC), and soil ammonium (NH_4^+-N) concentrations than *P. australis* marshes (all $p < 0.05$; Table 1).

Table 1
Soil physicochemical properties in different plant community and litter treatment. Data are shown as the means ± se (n = 5) and means followed by the same letter are not significantly difference ($p < 0.05$)

	P. australis		***S. alterniflora***	
	Control	**Litter removal**	**Control**	**Litter removal**
Temperature (℃)	24.3 ± 0.33 b	24.27 ± 0.43 b	25.23 ± 0.25 a	25.24 ± 0.13 a
Moisture (%)	37.67 ± 0.34 a	38.03 ± 0.25 a	36.53 ± 0.35 b	36.28 ± 0.26 b
pH	8.44 ± 0.04 a	8.27 ± 0.06 b	8.15 ± 0.04 bc	8.07 ± 0.07 c
Salinity (ppt)	1.22 ± 0.08 c	1.61 ± 0.04 b	1.98 ± 0.17 a	1.85 ± 0.13 ab
NH_4^+ (mg kg^{-1})	10.59 ± 0.85 bc	11.66 ± 1.3 b	19.97 ± 3.41 a	4.95 ± 1.04 c
NO_3^- (mg kg^{-1})	2.31 ± 2.07 a	4.28 ± 0.89 a	2.86 ± 1.06 a	2.72 ± 1.41 a
SOC (g kg^{-1})	0.96 ± 0.06 c	0.92 ± 0.02 c	1.46 ± 0.06 a	1.21 ± 0.06 b

Two-way ANOVA revealed significant interaction effects between plant community type and litter removal on soil salinity ($F = 4.75$, $p < 0.05$) and soil NH_4^+-N ($F = 17.04$, $p < 0.05$), and a marginally significant interaction effect on SOC ($F = 4.25$, $p = 0.056$; Table 2). Litter removal significantly increased soil salinity and decreased soil pH in *P. australis* marshes, but these parameters were unaffected by litter removal in *S. alterniflora* marshes (Table 2). For soil nutrients, litter removal significantly decreased soil NH + 4-N concentrations only in *S. alterniflora* marshes. It also led to a decrease in SOC in *S. alterniflora* marshes (though the interaction was marginal), while SOC in *P. australis* marshes was not significantly affected. Litter removal had no significant main or interactive effects on soil temperature, soil moisture, or soil nitrate (NO- 3-N) concentrations in either marsh type (Table 2).

Table 2
P-value of ANOVA for effect of litter removal (L) and type of salt marshes (T) on soil physicochemical properties. Bold fonts indicate significant difference ($p < 0.05$)

L	**Temperature**	**Moisture**	**pH**	**Salinity**	**NH + 4**	**NO- 3**	**SOC**
	0.973	**0.860**	**0.037**	**0.320**	**0.003**	**0.530**	**0.016**
T	**0.006**	**< 0.001**	**< 0.001**	**< 0.001**	0.503	0.731	**< 0.001**
L × T	0.954	0.330	0.374	**0.044**	**< 0.001**	0.468	0.056

Effects of plant community type and litter removal on plant growth

ANOVA results indicated significant interaction effects between plant community type and litter removal on ramet density ($F = 5.03$, $p < 0.05$) and AGB ($F = 10.20$, $p < 0.05$; Fig. 2). Litter removal had no significant effect on ramet density, plant height, or AGB of *P. australis* (Fig. 2a-c). In contrast, litter removal significantly increased ramet density in *S. alterniflora* by 21.4% ($p < 0.05$; Fig. 2a) and enhanced its AGB by 74.2% ($p < 0.05$; Fig. 2c). Plant height of *S. alterniflora* was not significantly affected by litter removal (Fig. 2b).

Effects of plant community type and litter removal on soil respiration

Overall, mean Rs throughout the growing season was significantly lower in *P. australis* marshes than in *S. alterniflora* marshes ($F = 15.04$, $p < 0.05$; Fig. 3c). Seasonal Rs in *S. alterniflora* marshes exhibited a wider range (0.12 to 15.2 μmol m^{-2} s^{-1}) compared to *P. australis* marshes (0.19 to 9.06 μmol m^{-2} s^{-1}) (Fig. 3a, b). Repeated-measures ANOVA revealed a significant interaction effect between plant community type and litter removal on Rs ($F = 13.42$, $p < 0.01$; Fig. 3c). Specifically, litter removal significantly decreased mean seasonal Rs in *P. australis* marshes by 38.3% (from 3.38 ± 0.07 to 2.08 ± 0.29 μmol m^{-2} s^{-1}; $p < 0.001$; Fig. 3a). Conversely, litter removal significantly increased mean seasonal Rs in *S. alterniflora* marshes by 25.9% (from 4.22 ± 0.20 to 5.31 ± 0.54 μmol m^{-2} s^{-1}; $p < 0.05$; Fig. 3b). The stimulatory effect of litter removal on Rs in S. alterniflora was particularly evident from August onwards (Fig. 3b).

Dynamics of litter decomposition

The results of the litter decomposition experiment showed that litter mass of *S. alterniflora* had lost 92.7%, while the litter of *P. australis* had lost 49.3% after 210 days (Fig. 4a). The decomposition rate of the litter of *S. alterniflora* (k = 0.014 day^{-1})was significantly higher than that of *P. australis* (k = 0.003 day^{-1}; Fig. 4b).

Relationship between soil respiration, plant growth, and soil physicochemical properties

General linear regression analysis revealed that the relationships between Rs and AGB or soil physicochemical properties differed between the two marsh types (Fig. 5). In *P. australis* marshes, Rs was negatively correlated with soil salinity (R^2 = 0.32, p < 0.05) and soil NH + 4-N (R^2 = 0.43, p < 0.05). No significant correlation was found between Rs and AGB in *P. australis* marshes (Fig. 5). In *S. alterniflora* marshes, Rs was positively correlated with AGB (R^2 = 0.33; p < 0.05). Conversely, Rs showed negative correlations with soil moisture (R^2 = 0.62; p < 0.001), soil salinity (R^2 = 0.32, p < 0.05), and soil NH + 4-N (R^2 = 0.61, p < 0.01; Fig. 5).

Discussion

While studies in many terrestrial ecosystems such as forests and grasslands have generally shown that litter removal decreases Rs by reducing organic matter and nutrient inputs (Joos et al. 2010, Keiblinger et al. 2010, Leitner et al. 2016), the role of plant litter in regulating Rs within salt marsh ecosystems has received considerably less attention. Our study revealed that the impact of litter removal on Rs in salt marshes is highly contingent on the dominant plant community. We observed contrasting effects: litter removal decreased Rs in native *P. australis* marshes but significantly increased Rs in marshes invaded by *S. alterniflora*. This divergence highlighted that the mechanisms by which litter influences Rs are intricately linked to vegetation-specific traits and their interaction with the unique abiotic conditions of salt marshes.

Mechanisms driving the decrease in Rs in P. australis marshes following litter removal

We hypothesized that litter removal might decrease the quantity of organic matter input, resulting in a reduction in Rs. However, the direction and magnitude of the effect on Rs were opposite in native and exotic salt marshes in this study. Consistent with previous studies (Sayer 2006, Kuzyakov 2010), litter removal decreased Rs in *P. australis* (Fig. 3). It should be emphasized that the reduction in Rs was likely not attributable to the traditional substrate limitation for microbial communities, as litter removal did not reduce AGB and SOC in *P. australis* (Table 1; Fig. 2c). Previous studies have demonstrated that Rs is strongly inhibited by indirect abiotic stress factor such as salinity (Chambers et al. 2013, Troxler et al. 2015). We detected significantly higher soil salinity after litter removal in *P. australis* marshes (Table 1), which negatively correlated with Rs in this study (Fig. 5). From these results, we infer that the increase in salinity is the primary factor suppressing Rs in *P. australis* following litter removal. We also found significant negative correlations between Rs and soil NH + 4 and moisture (Fig. 5). Elevated nitrogen levels in the soil inhibited plant fine root biomass, likely reducing root respiration intensity (Bae et al. 2012, Deegan et al. 2012). Increased soil moisture due to precipitation and evaporation may also decrease Rs (Fekete et al. 2015, Heim et al. 2021). However, the changes in soil moisture and NH + 4 in *P. australis* marshes were not a result of litter removal (Table 1). Therefore, the increased salinity resulting from litter removal may be the main reason for the decreased Rs in *P. australis* marshes.

Mechanisms driving the increase in Rs in S. alterniflora marshes following litter removal

For *S. alterniflora* salt marshes, the increase of Rs after litter removal was mainly mediated by promoting plant growth. The removal of litter reduced shading effects on plant growth, thereby increasing light availability within the canopy of *S. alterniflora*. As a C4 plant, *S. alterniflora* can effectively utilizes this enhanced light availability to optimize photosynthesis, thereby boosting its productivity, specifically reflected in the density and AGB (Fig. 2) (Xu et al. 2022). Increased AGB likely enhanced the transport of photosynthetic products from the surface to the ground, leading to a significant rise in the activity and quantity of microorganisms, therefore, increasing Rs. As shown in Fig. 3, the elevated Rs under litter removal was primarily driven by higher rates during the late growing season (Fig. 3). This may be attributed to ongoing decomposition of litter during growing season (April to July), which partially offset the difference in Rs between control and litter removal plot (Fig. 3b,4). Similar results have also been reported in a field observation that plant litter alteration had significant effect Rs (by microbial respiration mainly) from July to September in a semiarid grassland (Zhao et al. 2020). Unlike the previous study, the removal of litter in this study might have increased the input of fresh organic matter rather than decreased it, meanwhile, the priming effects caused by fresh substrate increased the microbial decomposition of pre-existing organic carbon (Kuzyakov et al. 2000). Litter removal significantly decreased soil NH + 4 and SOC, but these changes should not be the cause of Rs rise according to previous studies. The reduction in soil NH + 4 (Table 1) may be attributed to the changes in nitrogen input mode (Feng et al. 2022). While the slight decrease in SOC was likely a consequence of the increased Rs depleting existing organic carbon (Shahzad et al. 2015).

Implications of plant invasion for litter effects on soil respiration

Invasive plants often exhibit higher nitrogen use efficiency and productivity compared to native plants (Yang et al. 2013, Zhou et al. 2014, Huang et al. 2016, Uddin and Robinson 2018). Therefore, plant invasion alters the input pattern of soil organic matter in the original ecosystem through changes the quantity and quality of litter, exerting more obvious impact on the soil carbon and nitrogen cycle. The C4 plant *S. alterniflora* has a longer growing season and higher photosynthetic efficiency than the C3 plant *P. australis* (Jiang et al. 2009, Xu et al. 2022). Increased rates of photosynthesis and plant growth enhance the input of organic matter into the rhizosphere, stimulating microbial activity and resulting in elevated Rs in *S. alterniflora* marshes (Inglett et al. 2011, Poffenbarger et al. 2011). Additionally, The litter of *S. alterniflora* is of higher quality and more easily decomposed by microbe (Fig. 4)(Liao et al. 2008).

Although the decomposition of litter during the *S. alterniflora* invasion can increase the Rs of salt marsh soil, the accumulation of litter can also inhibit plant growth by shading light resources, thereby reducing Rs. Evidently, the mechanism by which litter affects Rs during plant invasion may be more complex than we expected and requires further research to explain.

Study limitations and future directions

This study has several limitations. Our single-year, single-site experiment cannot capture interannual and cross-site variability. We did not partition Rs components or characterize microbial communities, leaving mechanistic interpretations dependent on indirect evidence. The complete litter removal treatment also represents an extreme rather than a realistic scenario. Future studies employing multi-year, multi-site designs with isotopic partitioning and microbial analyses are needed to strengthen the conclusions drawn here.

Conclusions

To clarify the interaction effects of litter and plant invasion on Rs in salt marshes, we compared the short-term impacts of litter removal on Rs in native *P. australis* and exotic *S. alterniflora* marshes in the Yangtze River estuary. Our findings indicated that litter removal and *S. alterniflora* invasion significantly influenced Rs by altering soil properties and plant growth. Furthermore, the effects of litter on Rs varied considerably between *P. australis* and *S. alterniflora* salt marshes. Specifically, litter removal reduced Rs in *P. australis* marshes due to increased salinity, while it enhanced Rs in *S. alterniflora* by increasing AGB. We emphasized that the stimulation of *S. alterniflora* invasion on Rs may be partly restricted by litter coverage. From this, the role of litter to Rs depends on the type of vegetation, and plant invasion could alter this. This study enhances our understanding of the complex interactions among litter, soil properties, and plant community dynamics in regulating carbon cycling in salt marsh ecosystems.

Declarations

Ethics approval

No applicable.

Competing interests

The authors declare no conflict of interest.

Authors’ contributions

Songshuo Li: Conceptualization, Methodology, Formal analysis, Investigation, Resources, Data Curation, Writing – original draft, Writing – review & editing, Visualization. Hao Liu: Formal analysis, Investigation, Resources, Data Curation, Writing – original draft, Writing – review & editing. Chenhao Zhou: Methodology, Formal analysis, Validation. Zhang Yan: Formal analysis, Investigation, Methodology.

Visualization. Xiao Xu: Conceptualization, Data curation, Writing – review & editing, Validation. Jing Li: Formal analysis, Investigation. Yongcheng Ding: Methodology, Data Curation, Supervision. Qing Wang: Methodology, Data Curation, Supervision, Funding acquisition. Jianqiang Wu: Validation, Resources, Data Curation. Ming Nie: Conceptualization, Methodology, Supervision, Project administration. Min Wang: Validation, Supervision. Bo Li: Conceptualization, Supervision, Validation, Writing – review & editing. Project administration.

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Availability of data and material

Data will be made available on request.

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References

1. Bae, K., D. K. Lee, T. J. Fahey, S. Y. Woo, A. K. Quaye, and Y.-K. Lee. 2012. Seasonal variation of soil respiration rates in a secondary forest and agroforestry systems. Agroforestry Systems **87**:131-139.
2. Bethe, S. E., J. T. Weedon, J. Marinissen, M. P. Berg, and M. M. Hefting. 2025. Altered litter quality drives changes in litter decomposition following implementation of a regenerative measure in Dutch peat meadows. J Environ Manage **378**:124725.
3. Bond-Lamberty, B., V. L. Bailey, M. Chen, C. M. Gough, and R. Vargas. 2018. Globally rising soil heterotrophic respiration over recent decades. Nature **560**:80-83.
4. Bu, N., J. Qu, G. Li, B. Zhao, R. Zhang, and C. Fang. 2015. Reclamation of coastal salt marshes promoted carbon loss from previously-sequestered soil carbon pool. Ecological Engineering **81**:335-339.
5. Campbell, A. D., L. Fatoyinbo, L. Goldberg, and D. Lagomasino. 2022. Global hotspots of salt marsh change and carbon emissions. Nature **612**:701-706.
6. Chambers, L. G., T. Z. Osborne, and K. R. Reddy. 2013. Effect of salinity-altering pulsing events on soil organic carbon loss along an intertidal wetland gradient: a laboratory experiment. Biogeochemistry **115**:363-383.
7. Deegan, L. A., D. S. Johnson, R. S. Warren, B. J. Peterson, J. W. Fleeger, S. Fagherazzi, and W. M. Wollheim. 2012. Coastal eutrophication as a driver of salt marsh loss. Nature **490**:388-392.

8. Diagne, C., B. Leroy, A. C. Vaissiere, R. E. Gozlan, D. Roiz, I. Jaric, J. M. Salles, C. J. A. Bradshaw, and F. Courchamp. 2021. High and rising economic costs of biological invasions worldwide. Nature **592**:571-576.
9. Duarte, B., I. Caçador, J. C. Marques, and I. W. Croudace. 2013. Tagus estuary salt marshes feedback to sea level rise over a 40-year period: Insights from the application of geochemical indices. Ecological Indicators **34**:268-276.
10. Ehrenfeld, J. G. 2010. Ecosystem Consequences of Biological Invasions. Annual Review of Ecology, Evolution, and Systematics **41**:59-80.
11. Fan, J., R. Luo, B. G. McConkey, and N. Ziadi. 2020. Effects of nitrogen deposition and litter layer management on soil CO(2), N(2)O, and CH(4) emissions in a subtropical pine forestland. Sci Rep **10**:8959.
12. Fekete, I., Z. Kotroczó, C. Varga, P. T. Nagy, G. Várbíró, R. D. Bowden, J. A. Tóth, and K. Lajtha. 2014. Alterations in forest detritus inputs influence soil carbon concentration and soil respiration in a Central-European deciduous forest. Soil Biology and Biochemistry **74**:106-114.
13. Fekete, I., C. Varga, B. Biró, J. A. Tóth, G. Várbíró, K. Lajtha, G. Szabó, and Z. Kotroczó. 2015. The effects of litter production and litter depth on soil microclimate in a central european deciduous forest. Plant and Soil **398**:291-300.
14. Feng, J., Z. Li, Y. Hao, J. Wang, J. Ru, J. Song, and S. Wan. 2022. Litter removal exerts greater effects on soil microbial community than understory removal in a subtropical-warm temperate climate transitional forest. Forest Ecology and Management **505**.
15. Heim, R. J., W. Heim, G. F. Darman, T. Heinken, S. M. Smirenski, and N. Holzel. 2021. Litter removal through fire - A key process for wetland vegetation and ecosystem dynamics. Science of the Total Environment **755**:142659.
16. Hou, L., W. Kong, X. Tong, J. Liu, W. Li, M. Shao, X. Wang, and X. Wei. 2025. Effects of litter removal on grazing excluded grassland: A 5-year test with contrasting exclusion durations and topographic conditions. Agriculture, Ecosystems & Environment **393**.
17. Huang, J., X. Xu, M. Wang, M. Nie, S. Qiu, Q. Wang, Z. Quan, M. Xiao, and B. Li. 2016. Responses of soil nitrogen fixation to Spartina alterniflora invasion and nitrogen addition in a Chinese salt marsh. Scientific Reports **6**:20384.
18. Inglett, K. S., P. W. Inglett, K. R. Reddy, and T. Z. Osborne. 2011. Temperature sensitivity of greenhouse gas production in wetland soils of different vegetation. Biogeochemistry **108**:77-90.
19. Jiang, L., Y. Luo, J. Chen, and B. Li. 2009. Ecophysiological characteristics of invasive Spartina alterniflora and native species in salt marshes of Yangtze River estuary, China. Estuarine, Coastal and Shelf Science **81**:74-82.
20. Joos, O., F. Hagedorn, A. Heim, A. K. Gilgen, M. W. I. Schmidt, R. T. W. Siegwolf, and N. Buchmann. 2010. Summer drought reduces total and litter-derived soil CO_2 effluxes in temperate grassland - clues from a ^{13}C litter addition experiment. Biogeosciences **7**:1031-1041.

21. Keiblinger, K. M., E. K. Hall, W. Wanek, U. Szukics, I. Hammerle, G. Ellersdorfer, S. Bock, J. Strauss, K. Sterflinger, A. Richter, and S. Zechmeister-Boltenstern. 2010. The effect of resource quantity and resource stoichiometry on microbial carbon-use-efficiency. FEMS Microbiology Ecology **73**:430-440.
22. Kuzyakov, Y. 2010. Priming effects: Interactions between living and dead organic matter. Soil Biology and Biochemistry **42**:1363-1371.
23. Kuzyakov, Y., J. K. Friedel, and K. Stahr. 2000. Review of mechanisms and quantification of priming effects. Soil Biology and Biochemistry **32**:1485-1498.
24. Leff, J. W., W. R. Wieder, P. G. Taylor, A. R. Townsend, D. R. Nemergut, A. S. Grandy, and C. C. Cleveland. 2012. Experimental litterfall manipulation drives large and rapid changes in soil carbon cycling in a wet tropical forest. Global Change Biology **18**:2969-2979.
25. Leitner, S., O. Sae-Tun, L. Kranzinger, S. Zechmeister-Boltenstern, and M. Zimmermann. 2016. Contribution of litter layer to soil greenhouse gas emissions in a temperate beech forest. Plant and Soil **403**:455-469.
26. Li, Y., J. Zhang, E. Li, Y. Miao, S. Han, Y. Liu, Y. Liu, C. Zhao, and Y. Zhang. 2022. Changes in carbon inputs affect soil respiration and its temperature sensitivity in a broadleaved forest in central China. Catena **213**:106197.
27. Liao, C., Y. Luo, C. Fang, J. Chen, and B. Li. 2008. Litter pool sizes, decomposition, and nitrogen dynamics in Spartina alterniflora-invaded and native coastal marshlands of the Yangtze Estuary. Oecologia **156**:589-600.
28. Liao, C., Y. Luo, L. Jiang, X. Zhou, X. Wu, C. Fang, J. Chen, and B. Li. 2007. Invasion of Spartina alterniflora Enhanced Ecosystem Carbon and Nitrogen Stocks in the Yangtze Estuary, China. Ecosystems **10**:1351-1361.
29. Lin, Y. Z., Q. Q. Chen, Y. F. Qiu, R. R. Xie, H. Zhang, Y. Zhang, J. B. Li, and Y. H. Han. 2024. Spartina alterniflora invasion altered phosphorus retention and microbial phosphate solubilization of the Minjiang estuary wetland in southeastern China. J Environ Manage **358**:120817.
30. McLeod, E., G. L. Chmura, S. Bouillon, R. Salm, M. Björk, C. M. Duarte, C. E. Lovelock, W. H. Schlesinger, and B. R. Silliman. 2011. A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO2. Frontiers in Ecology and the Environment **9**:552-560.
31. Poffenbarger, H. J., B. A. Needelman, and J. P. Megonigal. 2011. Salinity Influence on methane emissions from tidal marshes. Wetlands **31**:831-842.
32. Rodtassana, C., and E. V. J. Tanner. 2018. Litter removal in a tropical rain forest reduces fine root biomass and production but litter addition has few effects. Ecology **99**:735-742.
33. Sayer, E. J. 2006. Using experimental manipulation to assess the roles of leaf litter in the functioning of forest ecosystems. Biological Reviews of the Cambridge Philosophical Society **81**:1-31.
34. Shahzad, T., C. Chenu, P. Genet, S. Barot, N. Perveen, C. Mougin, and S. Fontaine. 2015. Contribution of exudates, arbuscular mycorrhizal fungi and litter depositions to the rhizosphere priming effect induced by grassland species. Soil Biology and Biochemistry **80**:146-155.

35. Sharma, S., A. T. M. Rafiqul Hoque, K. Analuddin, and A. Hagihara. 2012. Litterfall dynamics in an overcrowded mangrove Kandelia obovata (S., L.) Yong stand over five years. Estuarine, Coastal and Shelf Science **98**:31-41.
36. Troxler, T. G., J. G. Barr, J. D. Fuentes, V. Engel, G. Anderson, C. Sanchez, D. Lagomasino, R. Price, and S. E. Davis. 2015. Component-specific dynamics of riverine mangrove CO_2 efflux in the Florida coastal Everglades. Agricultural and Forest Meteorology **213**:273-282.
37. Uddin, M. N., and R. W. Robinson. 2018. Can nutrient enrichment influence the invasion of Phragmites australis? Science of the Total Environment **613-614**:1449-1459.
38. Vivanco, L., I. C. Irvine, and J. B. Martiny. 2015. Nonlinear responses in salt marsh functioning to increased nitrogen addition. Ecology **96**:936-947.
39. Wang, F., M. Eagle, K. D. Kroeger, A. C. Spivak, and J. Tang. 2021a. Plant biomass and rates of carbon dioxide uptake are enhanced by successful restoration of tidal connectivity in salt marshes. Science of the Total Environment **750**:141566.
40. Wang, J., A. Zhang, Y. Zheng, J. Song, J. Ru, M. Zheng, D. Hui, and S. Wan. 2021b. Long-term litter removal rather than litter addition enhances ecosystem carbon sequestration in a temperate steppe. Functional Ecology **35**:2799-2807.
41. Wang, J., X. Zhang, M. Nie, C. Fu, J. Chen, and B. Li. 2008. Exotic Spartina alterniflora provides compatible habitats for native estuarine crab Sesarma dehaani in the Yangtze River estuary. Ecological Engineering **34**:57-64.
42. Wu, J., Q. Zhang, F. Yang, Y. lei, Q. Zhang, and X. Cheng. 2017. Does short-term litter input manipulation affect soil respiration and its carbon-isotopic signature in a coniferous forest ecosystem of central China? Applied Soil Ecology **113**:45-53.
43. Wu, Y., C. Wang, X. Zhang, B. Zhao, L. Jiang, J. Chen, and B. Li. 2008. Effects of saltmarsh invasion by Spartina alterniflora on arthropod community structure and diets. Biological Invasions **11**:635-649.
44. Xu, X., C. Zhou, Q. He, S. Qiu, Y. Zhang, J. Yang, B. Li, and M. Nie. 2022. Phenotypic plasticity of light use favors a plant invader in nitrogen-enriched ecosystems. Ecology **103**:e3665.
45. Yang, W., H. Zhao, X. Chen, S. Yin, X. Cheng, and S. An. 2013. Consequences of short-term C_4 plant *Spartina alterniflora* invasions for soil organic carbon dynamics in a coastal wetland of Eastern China. Ecological Engineering **61**:50-57.
46. Zerihun, A., and K. D. Montagu. 2004. Belowground to aboveground biomass ratio and vertical root distribution responses of mature Pinus radiata stands to phosphorus fertilization at planting. Canadian Journal of Forest Research **34**:1883-1894.
47. Zhang, X., Z. Song, Y. Wu, L. Wu, Q. Li, Q. Hao, S. Xia, Y. Wang, X. Ran, Y. Fang, and H. Wang. 2025. Ecological stoichiometry of carbon, nitrogen, phosphorus, and silicon in coastal salt marsh plants and its implications for carbon sink management. J Environ Manage **392**:126891.
48. Zhao, X., Y. Li, Z. Xie, and P. Li. 2020. Effects of nitrogen deposition and plant litter alteration on soil respiration in a semiarid grassland. Science of the Total Environment **740**:139634.

49. Zhou, L., S. Yin, S. An, W. Yang, Q. Deng, D. Xie, H. Ji, Y. Ouyang, and X. Cheng. 2014. *Spartina alterniflora* invasion alters carbon exchange and soil organic carbon in eastern salt marsh of China. CLEAN – Soil, Air, Water **43**:569-576.

Figures

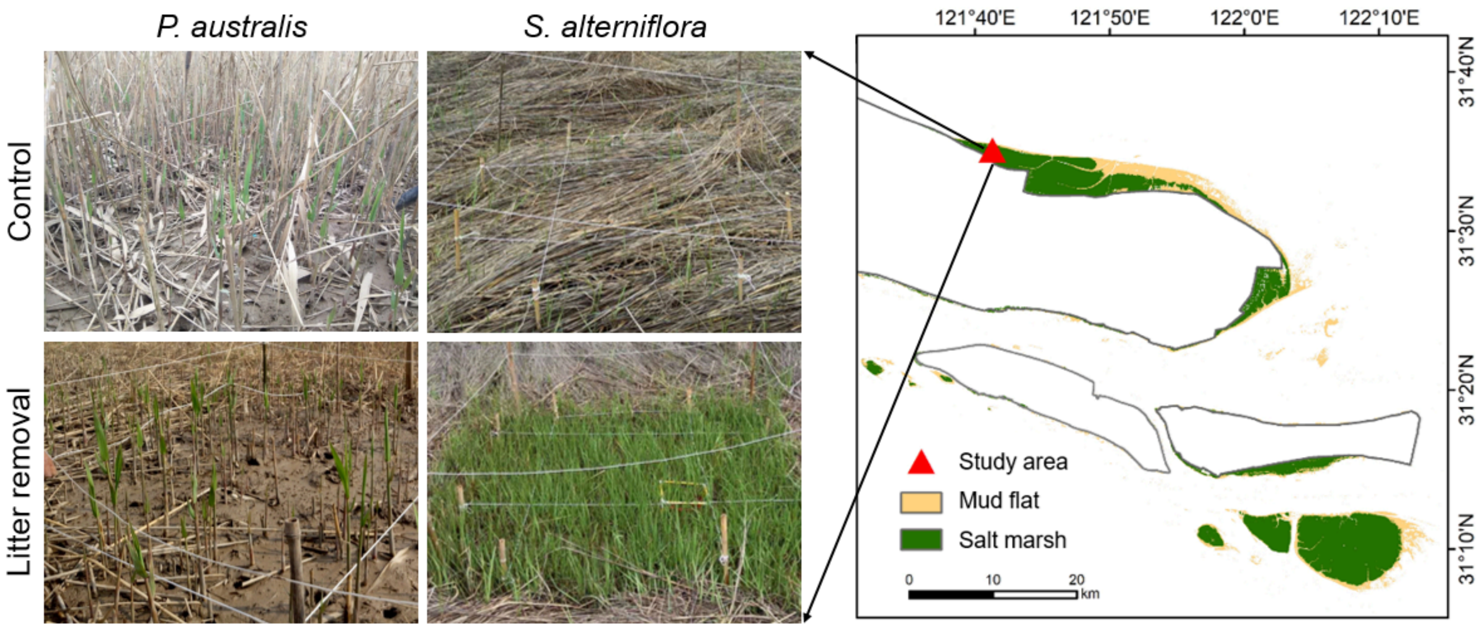

Figure 1

The locations of study sites and field experiment design

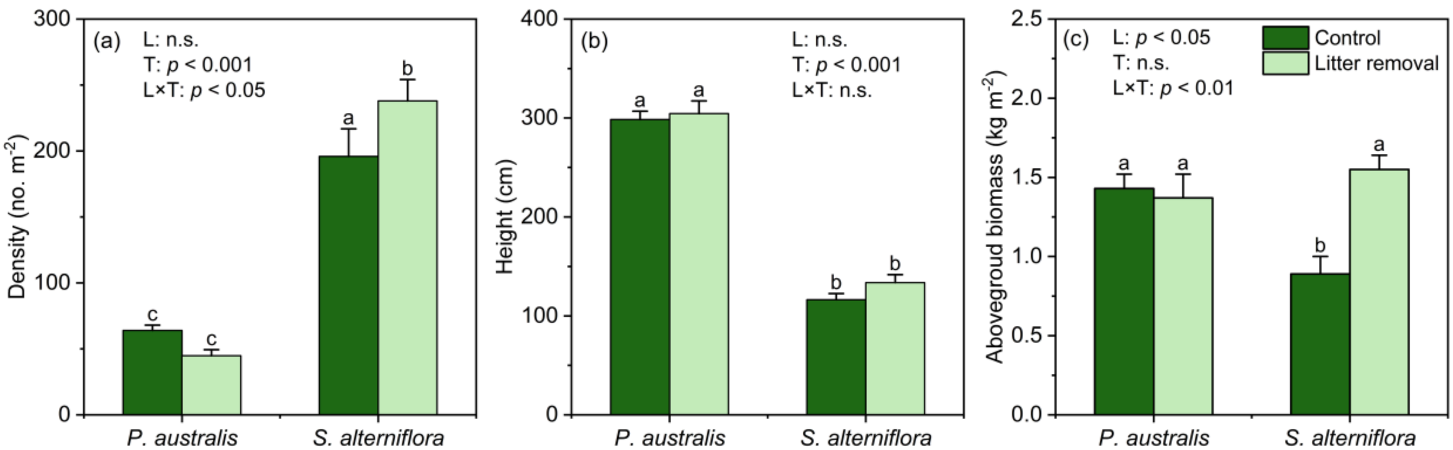

Figure 2

Effect of litter removal on density (a), height (b) and aboveground biomass (c) of *P. australis* and *S. alterniflora*. Data are shown as the means ± se (n = 5) and means followed by the same letter are not significantly difference ($p < 0.05$)

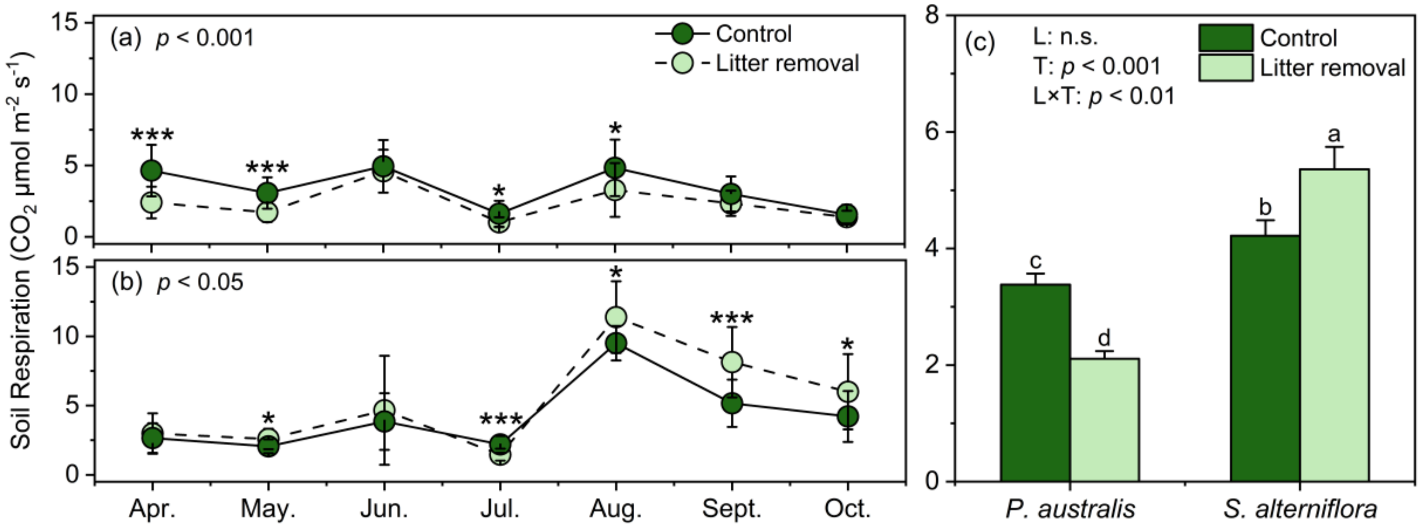

Figure 3

Seasonal dynamic of soil respiration in *P. australis* (a) and *S. alterniflora* (b) salt marshes, and effects of litter removal (L) and type of salt marshes (T) on annual average soil respiration (c). *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$. Data are shown as the means ± se (n = 5)

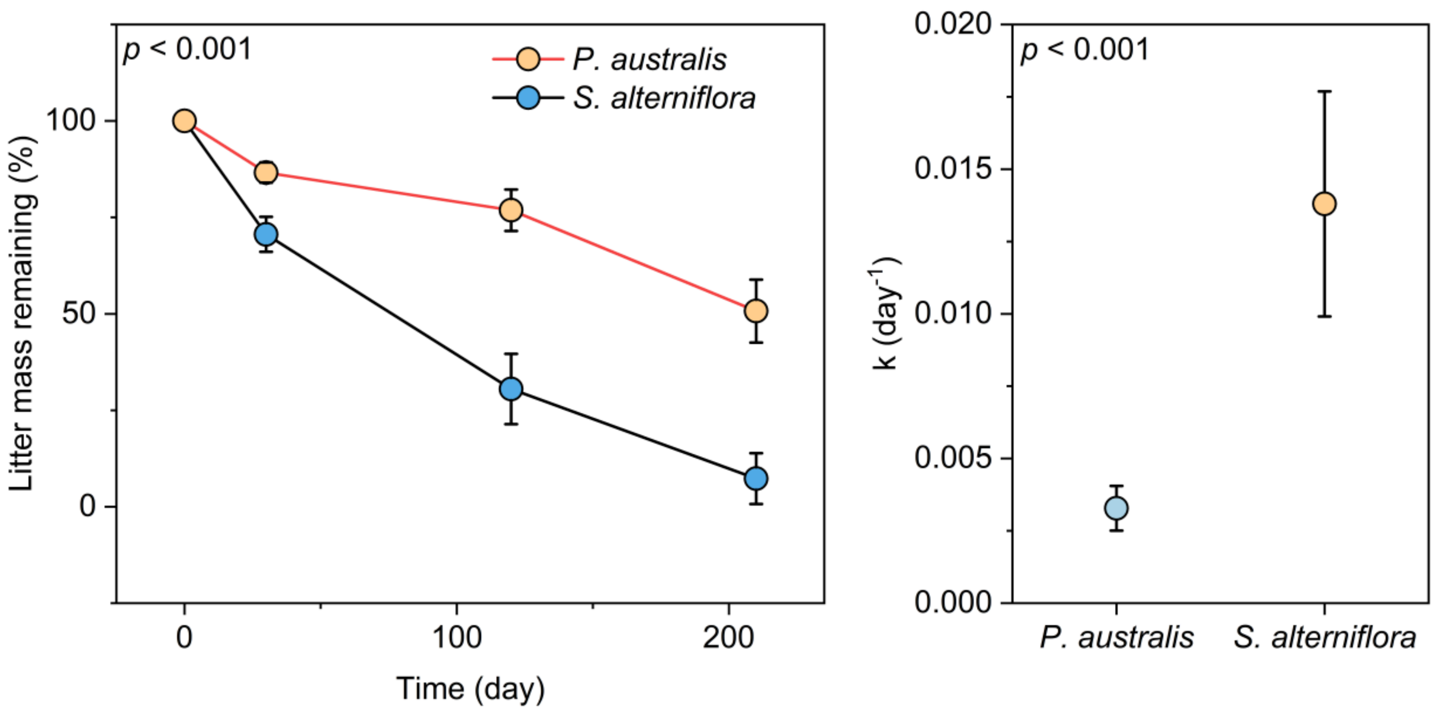

Figure 4

The Litter mass remaining and decomposition constant (k) of *P. australis* and *S. alterniflora*. Data are shown as the means ± se (n = 5)

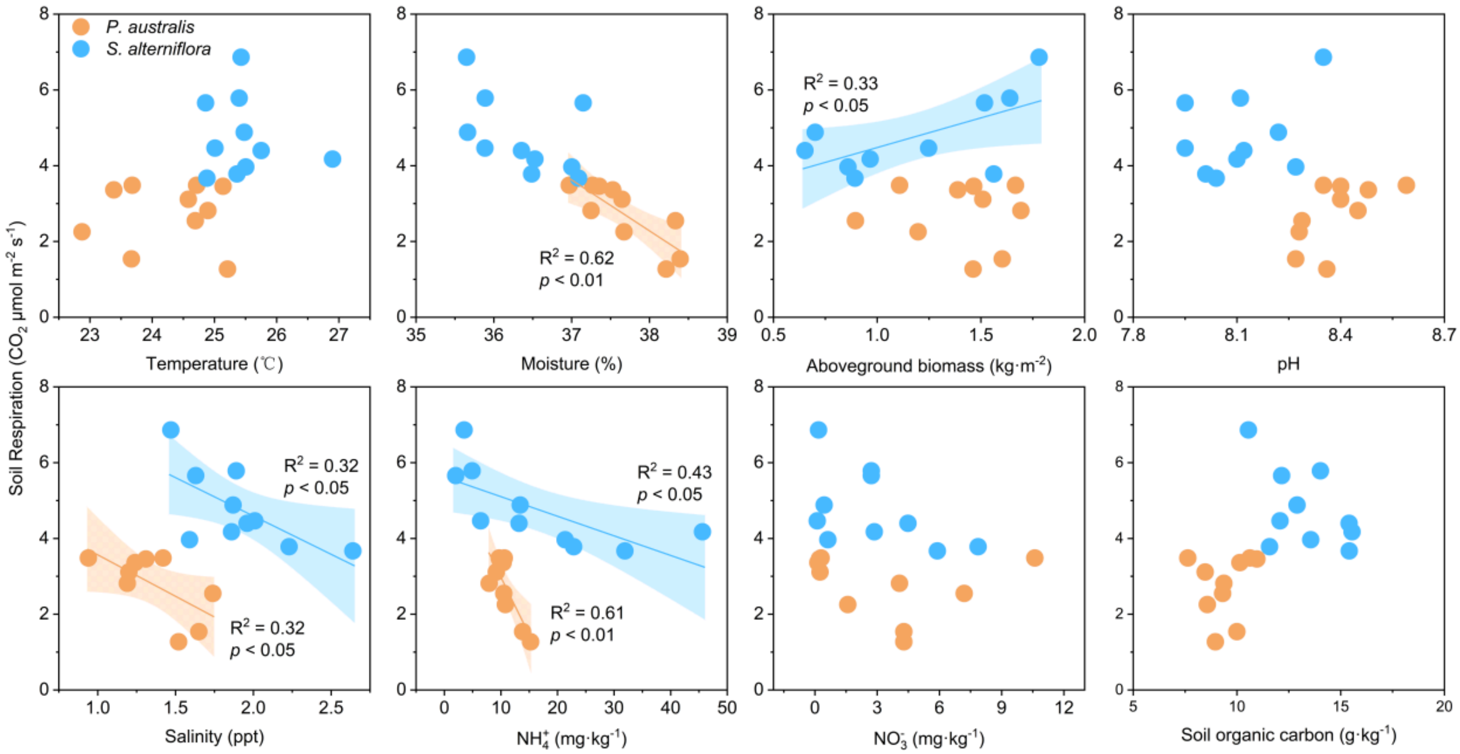

Figure 5

Relationship between aboveground biomass, soil physicochemical properties and soil respiration in *P. australis* and *S. alterniflora* salt marshes